radation by microbes in cecal contents increased (Fig. 1a). When halogeton was omitted from the diet, oxalate degradation rates again returned to pre-halogeton feeding levels. Similar results were obtained in another experiment with a different pig. In the latter experiment, rates of oxalate degradation by samples taken from the rectum were also measured. These rates were consistently higher than rates measured with samples taken concurrently from the cecum.

Rates of oxalate degradation by microbes in rectal contents from a horse (225 kg) increased after calcium oxalate was added to the diet, and then returned to low levels when calcium oxalate feeding was stopped (Fig. 1b). The highest rates measured were less than those in cecal samples from swine, rabbits, or guinea pigs. Oxalate degradation rates also increased in a similar experiment when halogeton rather than calcium oxalate was fed. In that experiment, halogeton intake was not well regulated because of problems associated with its palatability, and the data are not reported here.

Both CO_2 and formate are produced by oxalate decarboxylase (E.C. 4.1.1.2) from several species (*3*) and by strain OxB (*8*). When ^{14}C-labeled formate (10 m*M*) was incubated with gastrointestinal contents from each species studied here, rates of $^{14}CO_2$ production were much greater than oxalate degradation rates. Thus, ^{14}C from oxalate would not accumulate in formate, and we believe our measurements of $^{14}CO_2$ production from oxalate are reliable estimates of the potential or capacity for oxalate degradation by these populations.

Our measurements of oxalate degradation rates suggest that oxalate-degrading microbes are normally present in the large bowel of rabbits, guinea pigs, horses, and swine; and that concentrations of these oxalate degraders increase in response to the increased availability of oxalate. These results are similar to those obtained when increased dietary oxalate caused increased rates of oxalate degradation by ruminal microbes from sheep and cattle (*1*). It is likely that oxalate-utilizing bacteria are present in the gastrointestinal tracts of many animals.

Our inability to demonstrate selection of oxalate-degrading bacteria in the white rat agrees with results of Shirley and Schmidt-Nielsen (*7*). They found that significant quantities of ^{14}C from dietary ^{14}C-labeled oxalate were excreted as $^{14}CO_2$ by pack rats (*Neotoma albigula*), sand rats (*Psammomys obesus*), and hamsters (*Mesocricetus auratus*), but that this was not true with rats (*Rattus norvegicus*). The paucity of microbes with oxalate-degrading capacity in the intestine of the laboratory rat may be due to limited contact with other herbivores and a deficiency of oxalate (the substrate for the organisms) in the rat diet.

An isolate obtained by enrichment culture from cecal contents of an oxalate-adapted pig (*9*) appears to be identical to strain OxB obtained from the rumen. We propose that these bacteria or similar organisms are widely distributed and are more likely to be the agents of oxalate degradation in the large bowel than are any of the known bacteria that degrade oxalate under aerobic conditions.

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Dolphin Vocalization Mechanisms

Abstract. *Although humans have difficulty whistling when in a habitat that is more than 20 meters underwater, dolphins can make certain sounds at great depths through a related mechanism. Other dolphin sounds, such as clicks and complex buzzes, are produced by vibrations of the tissue of the nasal plugs, apparently without the use of the larynx; in these instances, the air sacs act as reservoirs. This was determined from studies of* Tursiops truncatus *and* Delphinus delphis *with harmless ultrasonic beams projected noninvasively to determine movements of the air sacs.*

About 340 B.C., Aristotle wrote that dolphins produce squeaks and moans (*1*). Since then various observers have described dolphin sounds as blats, bleats, chirps, clicks, creaks, pulses, quacks, racs, rasps, squeals, squawks, wails, and whistles (*2*). Considerable speculation exists about how small-toothed whales make sounds, such as simultaneous but independent whistles and clicks, without vocal cords and without blowing bubbles. Various mechanisms have been proposed (*3*), but a consensus has not been reached.

We projected into the heads of phonating dolphins narrow beams of low-intensity ultrasound at a frequency too high for them to hear; when aimed to reflect from moving surfaces of air spaces in the head, the sound returned was modified in frequency as measured by Doppler shifts. We thus determined which structures do and do not vibrate or otherwise move during sound production and modulation. We found, for example, that there are two general types of sounds, distinguished by whether or not tissue vibrations are involved in their generation, and that in dolphins the larynx does not seem to be involved in sound formation. Our procedures were noninvasive, harmless, did not disturb the animals, and could be done in or out of the water, thus leaving the acoustic situation normal.

Recently, the heads of dolphins have been explored by x-ray movies (*3*) and by pulsed ultrasonic imaging (*4*). Both imaging techniques involve periodic observations that are separated by insensitive intervals, and this intermittent "sampling" limits the rapidity of motion or the frequency that can be followed. Even a simple Doppler motion detector can follow the vibration of human vocal cords (*5*). To monitor motion in our studies, we used a modified commercial fetal heart monitor and its probe (*6*) as an ultrasonic source and receiver in some instances, and a special Doppler direction-resolving instrument (*7*) in other instances. The steady input of ultrasound at a frequency of 2 MHz is many times higher than the highest dolphin frequency; the subjects do not hear it directly but individual cycles of their sound movements can be recorded. The 2-MHz frequency produces a wavelength in soft tissue of 0.75 μm, and movements smaller than 10 μm can be observed in test

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objects. For gross movements, such as might be involved in modulation or air recycling, the usual Doppler frequency shift, which is proportional to velocity, is obtained (*4*) and, for small vibrations (amplitude $< \lambda/4$), the frequency observed is generally a mixture of f and $2f$, where f is the frequency of subject vibration (*8*). Because of the small, discrete wavelength involved, this monitoring process is not equivalent to "looking" into the head with a directional microphone; it gives better source resolution than does determining differences in arrival times at several contact microphones (*9*).

Dolphin anatomy was studied by dissecting several beached animals. Then observations were made on three Atlantic bottle-nose dolphins, *Tursiops truncatus*, and on two common dolphins, *Delphinus delphis*. The anatomy of the nasal passages of these animals has been described (*10*). In our study, we used the Doppler probe, which was held in contact with the dolphin's head at various positions (*11*) (Fig. 1). To observe the larnyx, we held the probe below the animal and aimed it up. The change in frequency returned relative to the outgoing frequency (Doppler shift frequency) was recorded as were the sounds produced by the animal. Both were then compared for temporal pattern of amplitude and for frequency analyzed into sound spectrograms.

Our observations indicated that the nasal plug and the air sacs (the vestibular, the nasofrontal, and the premaxillary sacs) all vibrate in synchronism with the clicking or buzz sounds while the larynx does not vibrate. The nasal diverticula on the right side vibrated with the clicking sound all the time, but on the left side, only some of the time. We observed that the vestibular sac was steadily inflated while the clicking sound was made. Vibrations appeared especially strong over the nasal plug toward the nodes. The vestibular sac, considered as a resonator, has an estimated size approximately corresponding to one of the buzz frequencies. The size changes during modulation. (The resonant frequency would change little if geometry were maintained by the transfer of air from the lungs as the animal swam down to a higher pressure region.) Vibrations were observed over much of the head, blowhole region, and on the internal air-tissue interfaces as the clicking sound was made. Even noninnervated structures vibrate in response to pressure variations on the surface. Air-filled structures can thus modify the radiated sound pattern, which is broad for the low frequencies,

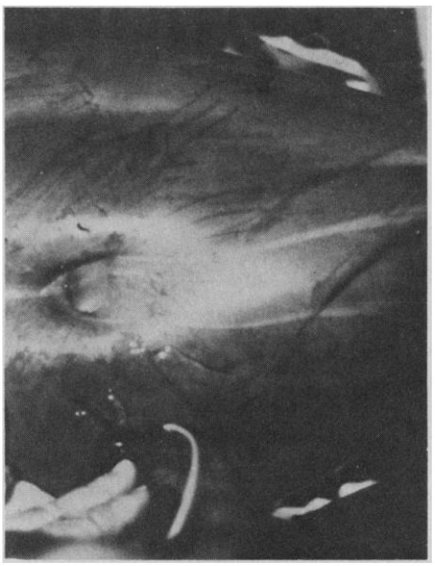

Fig. 1. The Doppler probe is hand-held in contact with the head of *Tursiops truncatus* near the blowhole in order to record rapid movement of the vestibular sac.

whose wavelengths are large with respect to the dimensions of the head, and more directed for the higher frequencies.

When humans whistle, tissue vibrations are not seen with this Doppler apparatus. Human whistling is imperfectly understood but has been described (*12*). As is the case with the teakettle whistle, the air vibrates but not because the solid structures guiding the air vibrate. At least one human (*13*) can whistle tunes through the nose with the mouth closed and vocal cords constricted to a slit; thus "internal" human whistles are not unknown. Most divers cannot whistle in habitats below 20 m. One of us (R.S.M.) can whistle tunes with difficulty at water depths of 30 m (4 atm) but can easily, at such depths, talk, "Bronx cheer," and blow bottles (panpipe flute) or rigid whistles, including "bird calls"; the last probably models human whistling (*14*). Because of this, we suspected that the whistles or pure tones that dolphins sometimes employ might involve an extension of the mechanism in which tissue vibrations would excite resonances, rather than use of an evolved air-vibration mechanism. Immunity to pressure quenching of a whistle seems to depend on the stiffness of the generating structure; increasing pressure increases the gas density but changes sound velocity little. When the dolphins whistled, no vibrations were detected either in the nasal diverticula or the larynx.

Gross movements of the larynx were not observed when either whistling or clicking sounds were made, nor were vibrations detected, but motion in the larynx could be detected with each breath. The x-ray spot films did not show larynx motion during respiration but did suggest that sound production was not present (*15*). Lack of vibration suggests that buzz sounds do not originate in the larynx. With regard to whistles, if the larynx provided part of a resonant system for their production, then gross motion would be expected during frequency modulation. These particular animals did not modulate the frequency of their whistles over a large range, but gross motion probably would have been detected if it had been present.

Much of the vocal activity of dolphins consists of clicks or a rapid succession of clicks merging into a cry. Different sounds involving rapid pulse repetition seem to be produced by the same conditions in the soft structure of the head. Dolphins can generate sounds in other ways, just as humans can speak or whistle while breathing in. (The unusual may sometimes recur as when Swedish women inhale while saying the word for yes.)

It appears from our observations that vibration of the nasal plugs probably is the originator, during upward airflow, of the clicking or buzz sounds. This source is consistent with electromyographic observations (*16*) and with the x-ray studies (*3*). The flow direction matches the x-ray observations of Norris *et al.* (*17*) but is opposite to Norris' earlier conjecture (*18*). When the blowhole is closed, air is recycled to the vestibular sac. The right side of the nasal diverticula was the primary site of the generation of clicks, although the left side was sometimes involved. The larynx probably is not involved in forming sounds. This observation is in agreement with some workers and not with others (*3*). There appear to be two general types of sound; one is generated by tissue vibrations, and the other is not. The whistle is produced by some edge- or hole-tone, vortex-shedding mechanism related to that used by humans. Humans use the vibration of the vocal cords in speech and a different mechanism to whistle; although humans usually do not make both sounds simultaneously, it is possible for most to do so (*19*).

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Metabolic Mapping of Functional Activity in Human Subjects with the [^{18}F]Fluorodeoxyglucose Technique

Abstract. *The 2-[^{18}F]fluoro-2-deoxy-D-glucose technique was used to measure regional cerebral glucose utilization by human subjects during functional activation. Normal male volunteers subjected to one or more sensory stimuli (tactile, visual, or auditory) exhibited focal increases in glucose metabolism in response to the stimulus. Unilateral visual hemifield stimulation caused the contralateral striate cortex to become more metabolically active than the striate cortex ipsilateral to the stimulated hemifield. Similarly, stroking the fingers and hand of one arm with a brush produced an increase in metabolism in the contralateral postcentral gyrus, compared with the homologous ipsilateral region. The auditory stimulus, which consisted of a monaurally presented factual story caused an increase in glucose metabolism in the auditory cortex in the hemisphere contralateral to the stimulated ear. These results demonstrate that the technique is capable of providing functional maps in vivo related to both body region and submodality of sensory information in the human brain.*

Using the recently developed 2-[^{18}F]-fluoro-2-deoxy-D-glucose (FDG) technique (*1*) for measuring local cerebral glucose metabolism we have determined which areas of the brain are activated by a specific sensory stimulus, thus enabling brain function to be mapped in vivo. The classical techniques for measuring human cerebral metabolism (*2*) do not provide regional data. We have now measured local cerebral metabolic rates for glucose in a series of volunteers subjected to a variety of specific sensory stimuli (*3*).

We measured the regional brain activity of both FDG and 2-[^{18}F]fluoro-2-deoxy-D-glucose-6-phosphate (FDG6P) with position emission transaxial tomographs [PETT III and PETT V (*4–7*)] and determined the arterial time course of ^{18}F and glucose from arterial blood samples drawn after the FDG injection. With these data and knowledge of certain constants of the FDG model, we calculated the metabolic rate of glucose in various regions of the brain (*1, 1a*).

Twenty-seven healthy men (20 to 28 years old) were subjects in the experiment. After radial artery catheterization under local anesthesia, each was made comfortable in the tomograph, and the head was secured with a foam head restraint. The head was extended to make the scan plane parallel to the orbital-meatal (OM) line defined as the plane through the lateral canthus and the external auditory meatus. Each volunteer was subjected to a tactile, a visual, or an auditory stimulus (*8*).

The tactile stimulus consisted of rapid but light stroking (2 to 3 Hz) of the volar and dorsal surface of the fingers and hand of one arm (left, $N = 2$; right, $N = 3$) with a hand-held brush, which was just stiff enough to cause an appreciable stimulus without causing any discomfort. Subjects were blindfolded to eliminate visual input and wore earplugs to minimize auditory input.

In the visual study, either the left ($N = 4$) or right ($N = 6$) visual hemifield was stimulated so as to ensure only hemifield stimulation (*9*). The stimulus consisted of a well-illuminated, slowly moving, high-contrast black-and-white pattern of small lines at various orientations as well as abstract color images presented into one visual hemifield. The subjects wore earplugs.

The auditory system was studied in six subjects with normal hearing (*10*) who listened to a tape-recorded factual story presented through earphones to only one ear (left ear, $N = 3$; right ear, $N = 3$) (*11*). Attentiveness to the story was assessed by testing the subject's recall. These subjects were also blindfolded.

Six subjects that were blindfolded and wore earplugs acted as controls for all the studies.

Section scans were started 30 minutes after the FDG injection (*12*). Each scan took 10 to 14 minutes, depending on the count rate, and six to eight scans were obtained at 1-cm levels through the region of interest of the brain. Quantification of metabolic rates (*13*) was performed as discussed by Reivech *et al.* (*1*).

The somatosensory input caused the postcentral gyrus contralateral to the stimulus to become metabolically more active (mean ± standard deviation, 9 ± 10.2 percent) than the homologous area in the ipsilateral cortex (Fig. 1). This was not significantly different from the controls [1 ± 6.8 percent, $t(9) = 1.5$, $P > .1$]. The nonsignificance is due to the large variance in the control subjects at the level of the postcentral gyrus.

The visual stimulus caused the visual cortex contralateral to the stimulated hemifield to become 8 ± 3.0 percent more active that the ipsilateral visual cortex (Fig. 2). The asymmetry is significant in comparison with the controls [$t(14) = 4.06$, $P < .01$], who showed a left-right asymmetry of only 0.5 ± 3.0 percent.

The monaurally presented auditory stimulation elevated the metabolic rate in the temporal cortex contralateral to the stimulated ear (Fig. 3). This cortex had a metabolic rate of 7 ± 2.5 percent higher than the ipsilateral temporal cortex. This asymmetry is significant in comparison with the controls [$t(8)$

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